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Professor Boris Sket (1936–2023): the SpeleoBiologist and much more

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Professor Boris Sket (Fig. 1) passed away on May 7, 2023, in Ljubljana at age 86. Many of us will remember him as a great naturalist, with a broad interest in zoology, botany, evolution, ecology, biogeography, and his main passion: subterranean fauna. Ashes to ashes; however, his research legacy remains. It is our honor to look back on his life and work to say goodbye.

To truly grasp and appreciate his nearly seven decades of research, we must journey back to the aftermath of the Second World War, when the map of Europe was redrawn. The Kingdom of Yugoslavia underwent a formal transformation into the Socialist Federative Republic of Yugoslavia led by communist party. Although the Yugoslavian communist regime cannot compare to much harsher communist rulers in countries of Eastern Europe, the nation faced economic challenges, less porous borders, and greater difficulty in communicating with the outside world compared to today. Nonetheless, Yugoslavia encompassed almost the entire Dinaric Karst, nowadays well known as a global hotspot of subterranean biodiversity. Exploration of caves was at that time already established and much of this exploration was led by biologists (Sket 2008a); however, large parts of the territory were unexplored at that time and much of the fauna was unknown.

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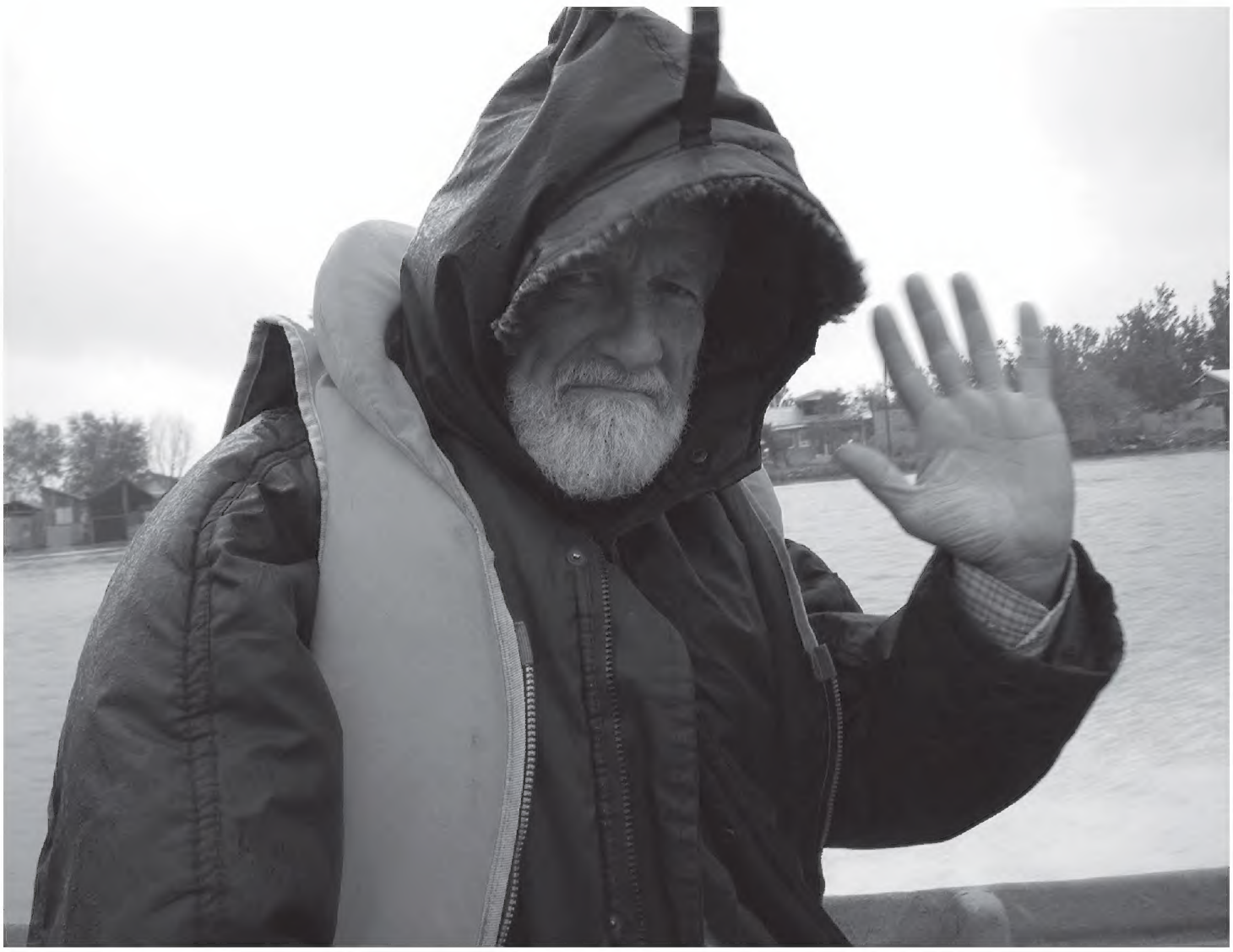

Figure 1. Boris Sket, 1936–2023 (Photo: Boris Sket archive).

Young Boris became acquainted with subterranean fauna early, amidst the turmoil of war, when Ljubljana was occupied and surrounded by barbed wires. During that period, he frequented the National Museum in Ljubljana (today Slovenian Museum of Natural History), where his attention was captured by two preserved specimens of subterranean crustaceans of the genera *Niphargus* and *Troglocaris*. Immediately following the war, he embarked on cycling expeditions with his grandfather to smaller caves in the vicinity of Ljubljana, where he was fascinated by whitish animals, most likely *Niphargus*. His early education was marked by frequent relocations between Ljubljana and Belgrade. Boris' professional journey into the exploration of subterranean life truly began with his enrollment at the University of Ljubljana, and his subsequent role as a teaching assistant to Professor Janez Matjašič (Box 1, Fig. 2).

The fieldwork activities at that time were far more time-consuming and relied heavily on improvisation compared with modern practices. Transportation options were limited, and commonly relied on trains and bicycles. The caving equipment was less sophisticated and under the development: the clothing resembled that of mountaineers, carbide flames preceded the powerful LED lamps of today, ladders ruled before ropes, homemade masks, pipes and air pumps were utilized before the advent of scuba diving gear. Nets, sieves, and filters were crafted at home with the assistance of his technical assistant, the malacologist and close friend France Velkovrh. One of Boris's most notable

Figure 2. Timeline of Boris Sket. Upper left: just arrived in 1936. Upper right: serving army near Valjevo, Serbia. Bottom: sampling interstitial near Ulcinj, Montenegro. (Photo: Boris Sket archive).

inventions was the so called "Sket bottle" (Chevaldonné et al. 2008; Sket 2018), a cleverly designed plastic bottle used for animal suction during snorkeling or diving. This period of field work importantly contributed to the accumulation of empirical evidence that the subterranean environment extends beyond caves, encompassing both the fissure systems of consolidated cracked carbonate rock and unconsolidated riverine sediments.

The Yugoslav regime was supporting nature exploration, although there was no imperative for publishing results. Much of Boris' research results from that period was documented in what is now termed "grey literature". Some of his findings were disseminated at international conferences and subsequently published in conference proceedings. Reports of his studies were submitted in multiple copies to funding authorities in Slovene language. Despite the absence of pressure to publish internationally, Boris' research opus is impressive, both in terms of breadth and depth. His attitude toward life and work can be summarized in three words: passion, curiosity, and persistence. He was a biologist *par excellence*, a researcher of numerous interests, ranging from pure nature observation through the lens of a camera to taxonomy, ecology, evolution, and

Box 1. The academic career of Boris Sket.

Education:

1961: PhD thesis entitled "Specialization of our freshwater isopods"; University program in Ljubljana (at that time named as Prirodoslovno-matematična fakulteta)

Employment:

1959–1969: Teaching assistant of professor Janez Matjašič.
1969–1974: Assistant professor for the zoology and speleobiology.
1974–2005: Full professor for the zoology and speleobiology
2005–2013: Researcher.
2013–2023: Retired yet active.

Mentorship:

10 PhD students
5 MSc students
25 Graduate students

Professional activities at the University:

1974–2012: Leader of the Research group for invertebrate zoology and speleobiology
1981–1983: Vice-dean of the Biotechnical Faculty at the University of Ljubljana.
1983–1985: Dean of the Biotechnical Faculty at the University of Ljubljana.
1985–1987: Vice-dean of the Biotechnical Faculty at the University of Ljubljana.
1989–1991: Rector of the University of Ljubljana.

Other professional activities:

1976–1980: President of Caving Society of Slovenia.
1998–2011: Leader of research Program "Zoology and speleobiology" (P1–0184, funded by Slovenian Research Agency).
2004–2008: President of the International Society for Subterranean Biology.
2011–2023: A member of Slovenian Academy of Science and Arts
2009–2023: A member of Bosnian Academy of Science and Arts

Awards:

Student's award of France Prešern.
1965: Award of Boris Kidrič.
1979: Order of labor, third class (silver wreath).
1988: Honorary member of Yugoslavian Cave association.
1991: Order of republic, third class (silver wreath).
1995: Jesenko Award of Biotechnical Faculty of University of Ljubljana.
2003: Zois Award for scientific excellence.
2008: Golden award of Slovenian Caving Association.
2010: Award for life work of Miroslav Zei of the National Institute of Biology.
2016: Honorary membership of the International Society of Speleobiology.

Editorial activities:

1997–2022: Acta Biologica Slovenica
2002–2023: Subterranean Biology
2005–2023: Zootaxa

Research output:

Over 350 articles
Over 570 bibliographic units (source: Slovenian bibliographic database)

conservation. While he was interested in both surface and subterranean life, the majority of his research efforts were dedicated to the latter. Over his long and fruitful life, he witnessed the transformation of the Dinaric Karst: from the pristine natural state during the pioneering years, to expanding urbanization, river channelization, damming and general degradation of the environment.

His contribution to science is impressive. Sometimes, he acted as the leading researcher, sometimes as a provider of data and ideas, and sometimes as a knowledgeable peer with immense field experience. Above all, he was a dedicated teacher who passed on his knowledge to successive generations of biologists of all formats and specializations. Here, we broadly expose his contributions to science, including work of his collaborators and students. We divided his opus into five arbitrary topic sections and a box summarizing his academic career.

Taxonomy & natural history

Many researchers will remember Boris as a taxonomist of broad interests, delving into the taxonomy of species across numerous phyla. According to his own words, his taxonomic expertise was "an unwanted need rather than his primary research interest" on a way to comprehend the subterranean Dinaric fauna. Taxonomic descriptions were the *sine qua non* for the rest of his work. Indeed, many discoveries of Dinaric species can be attributed to his research efforts.

Boris advocated a pragmatic use of the biological species concept, wherein morphological characters served as hints to potential or actual reproductive barriers. He maintained skepticism towards the uncritical usage of the term "cryptic species" asserting that genuine morphological crypticity could not be reliably distinguished from inadequate morphological examination. He was playful and humorous in naming new species: the black olm was named "parkelj", which is the Slovenian name of a traditional infernal figure accompanying St. Nicholas. Black with a red tongue, it resembles the black and red color combination in the non-troglomorphic morph of the olm. His main taxonomical contributions are outlined in five subsections, and the list of taxa he described is available in Table 1.

Annelida: Clitellata

Findings of leeches in Dinaric caves had two important consequences for Boris. First, he became one of the few global authorities in leech taxonomy, who curated several regional and global leech checklists (Sket 1986c; Sket and Trontelj 2008; Minelli et al. 2014), and served as a subject editor at Zootaxa. He studied distribution, ecology and taxonomy of glossiphoniid (Sket 1968), piscicolid (Sket 1985b) and several erpobdellid leeches (Sket 1968, 1981c; Sket and Šapkarev 1986; Sket 1989, 1992b), including the peculiar *Croatobrancus mestrovi* from deep caves of Velebit (Sket et al. 2001).

Table 1. List of taxa described by Boris Sket. Families and genera are described with G and F, respectively.

Classification	Taxon described	Category
Porifera		
Spongillidae	*Eunapius subterraneus* Sket & Velikonja, 1984	
Cnidaria		
Hydrozoa:	***Velkovrhia*** Matjašič & Sket, 1971	**G**
Bougainvilliidae	*Velkovrhia enigmatica* Matjašič & Sket, 1971	
Annelida: Clitellata: Rhynchobdellida		
Erpobdellidae	*Dina eturpshem* Sket, 1989	
	Dina krasensis (Sket, 1968)	
	Dina krilata Sket, 1989	
	Dina lepinja Sket & Šapkarev, 1986	
	Dina dinarica Sket, 1969	
	Dina lacustris Sket, 1970	
	Dina montana Sket, 1971	
	Dina ohridana Sket, 1968	
	Dina svilesta Sket, 1989	
	Trocheta dalmatina Sket, 1968	
Glossiphoniidae	*Glossiphonia complanata maculosa* Sket, 1968	
	Glossiphonia pulchella (Sket, 1968)	
Piscicolidae	*Cystobranchus pawlowskii* Sket, 1968	
	Piscicola hadzii Sket, 1985	
Arthopoda: Malacostraca		
Decapoda		
Atyidae	***Ficticaris*** Sket & Zakšek in Jugovic, Zakšek, Petković & Sket, 2019	**G**
	Ficticaris serbica Jugovic & Sket in Jugovic, Zakšek, Petković & Sket, 2019	
	Gallocaris Sket & Zakšek, 2009	**G**
	Spelaeocaris kapelana Sket & Zakšek, 2009	
	Spelaeocaris neglecta Sket & Zakšek, 2009	
	Spelaeocaris prasence Sket & Zakšek, 2009	
	Troglocaris anophthalmus legovici Jugovic, Jalžić, Prevorčnik & Sket, 2012	
	Troglocaris anophthalmus ocellata Jugovic, Jalžić, Prevorčnik & Sket, 2012	
	Troglocaris anophthalmus periadriatica Jugovic, Jalžić, Prevorčnik & Sket, 2012	
	Troglocaris anophthalmus sontica Jugovic, Jalžić, Prevorčnik & Sket, 2012	
	Troglocaris bosnica Sket & Zakšek, 2009	
Gecarcinucidae	*Sundathelphusa boex* Ng & Sket, 1996	
	Sundathelphusa sottoae Ng & Sket, 1996	
	Sundathelphusa urichi Ng & Sket, 1996	
	Sundathelphusa vedeniki Ng & Sket, 1996	
Amphipoda		
Anisogammaridae	***Fuxiana* Sket, 2000**	***G***
	Fuxiana yangi Sket, 2000	
	***Fuxigammarus* Sket & Fišer, 2009**	***G***
	Fuxigammarus antespinosus Sket & Fišer, 2009	
	Fuxigammarus barbatus Sket & Fišer, 2009	
	Fuxigammarus cornutus Sket & Fišer, 2009	
Bogidiellidae	*Bermudagidiella bermudiensis* (Stock, Sket & Iliffe, 1987)	
	Bogidiella gammariformis Sket, 1985	
	Bogidiella sinica Karaman & Sket, 1990	
Gammaridae	***Dinarogammarus* Sket & Hou, 2018**	***G***
	***Relictogammarus* Hou & Sket, 2016**	***G***
	***Iberogammarus* Sket & Hou, 2018**	***G***
	Gammarus parvioculatus Sidorov, Hou & Sket, 2018	
	Gammarus troglomorphus Sidorov, Hou & Sket, 2018	
	Neogammarus gordankaramani (Özbek & Sket, 2020)	

Classification	Taxon described	Category
Crangonyctidae	*Tadzocrangonyx alaicus* Sidorov, Hou & Sket, 2018	
Melitidae	*Melita mirzajanii* Krapp-Schickel & Sket, 2015	
Niphargidae	***Carinurella* Sket, 1971**	***G***
	Carinurella paradoxa (Sket, 1964)	
	***Chaetoniphargus* Karaman G.S. & Sket, 2019**	***G***
	Chaetoniphargus lubuskensis Karaman G.S. & Sket, 2019	
	***Niphargobates* Sket, 1981**	***G***
	Niphargobates orophobata Sket, 1981	
	Niphargobatoides lefkodemonaki (Sket, 1990)	
	Niphargus aberrans Sket, 1972	
	Niphargus brevirostris Sket, 1971	
	Niphargus carniolicus Sket, 1960	
	Niphargus dabarensis Fišer, Trontelj & Sket, 2006	
	Niphargus dobati Sket, 1999	
	Niphargus factor Sket & G. Karaman, 1990	
	Niphargus jadranko Sket & G. Karaman, 1990	
	Niphargus labacensis Sket, 1957	
	Niphargus liburnicus G. Karaman & Sket, 1989	
	Niphargus lourensis Fišer, Trontelj & Sket, 2006	
	Niphargus microcerberus Sket, 1972	
	Niphargus minor Sket, 1957	
	Niphargus multipennatus Sket, 1957	
	Niphargus numerus G. Karaman & Sket, 1990	
	Niphargus pachytelson Sket, 1960	
	Niphargus pectencoronatae Sket & G. Karaman, 1990	
	Niphargus pectinicauda Sket, 1971	
	Niphargus polymorphus Fišer, Trontelj & Sket, 2006	
	Niphargus pretneri Sket, 1959	
	Niphargus pupetta (Sket, 1962)	
	Niphargus rejici Sket, 1958	
	Niphargus rostratus Sket, 1971	
	Niphargus scopicauda Fišer, Coleman, Zagmajster, Zwittnig, Gerecke & Sket, 2010	
	Niphargus stenopus Sket, 1960	
	Niphargus subtypicus Sket, 1960	
	Niphargus transitivus Sket, 1971	
	Niphargus trullipes Sket, 1958	
	Niphargus vinodolensis Fišer, Sket & Stoch, 2006	
Pseudoniphargidae	*Pseudoniphargus carpalis* Stock, Holsinger, Sket & Iliffe, 1986	
	Pseudoniphargus grandimanus Stock, Holsinger, Sket & Iliffe, 1986	
Seborgiidae	*Seborgia kanaka* Jaume, Sket & Boxshall, 2009	
	Seborgia sanctensis Jaume, Sket & Boxshall, 2009	
	Seborgia vietnamica Jaume, Sket & Boxshall, 2009	
Ingolfiellidae	*Ingolfiella* (*Tethydiella*) *longipes* Stock, Sket & Iliffe, 1987	
Isopoda		
Anthuridae	*Stygocyathura filipinica* (Botosaneanu & Sket, 1999)	
Asellidae	*Asellus* (*Asellus*) *aquaticus carniolicus* Sket, 1965	
	Asellus (*Asellus*) *aquaticus cyclobranchialis* Sket, 1965	
	Asellus (*Asellus*) *aquaticus irregularis* Sket, 1965	
	Asellus (*Asellus*) *aquaticus longicornis* Sket, 1965	
	Proasellus anophtalmus bosnicus (Sket, 1965)	
	Proasellus coxalis nanus Sket, 1990	
	Proasellus deminutus (Sket, 1959)	
	Proasellus intermedius intermedius (Sket, 1965)	
	Proasellus orientalis (Sket, 1965)	

Classification	Taxon described	Category
Asellidae	*Proasellus parvulus* (Sket, 1960)	
	Proasellus slavus histriae (Sket, 1963)	
	Proasellus slavus serbiae (Sket, 1963)	
	Proasellus slavus styriacus (Sket, 1963)	
	Proasellus slavus zeii (Sket, 1963)	
	Proasellus slovenicus (Sket, 1957)	
	Proasellus vulgaris (Sket, 1965)	
	Remasellus Bowman & Sket, 1985	
Atlantasellidae	***Atlantasellidae* Sket, 1979**	***F***
	***Atlantasellus* Sket, 1979**	***G***
	Atlantasellus cavernicolus Sket, 1979	
Brasileirinidae	***Brasileirinidae* Prevorčnik, Ferreira & Sket, 2012**	***F***
	***Brasileirinho* Prevorčnik, Ferreira & Sket, 2012**	***G***
	Brasileirinho cavaticus Prevorčnik, Ferreira & Sket, 2012	
Cirolanidae	*Sphaeromides virei mediodalmatina* Sket, 1964	
	Sphaeromides virei montenigrina Sket, 1957	
	Turcolana lepturoides Prevorčnik, Konec & Sket, 2016	
Lepidocharontidae	*Microcharon luciae* Sket, 1990	
Protojaniridae	*Anneckella srilankae rectecopulans* Sket, 1982	
	Anneckella srilankae srilankae Sket, 1982	
	Enckella lucei major Sket, 1982	
Sphaeromatidae	***Bilistra* Sket & Bruce, 2004**	***G***
	Bilistra cavernicola Sket & Bruce, 2004	
	Bilistra millari Sket & Bruce, 2004	
	Bilistra mollicopulans Sket & Bruce, 2004	
	***Merozoon* Sket, 2012**	***G***
	Merozoon vestigatum Sket, 2012	
	Monolistra (*Microlistra*) *bolei* (Sket, 1960)	
	Monolistra (Microlistra) bolei bolei (Sket, 1960)	
	Monolistra (*Microlistra*) *bolei brevispinosa* Sket, 1982	
	Monolistra (*Microlistra*) *calopyge* Sket, 1982	
	Monolistra (*Microlistra*) *fongi* Prevorčnik, Verovnik, Zagmajster & Sket, 2010	
	Monolistra (*Microlistra*) *jalzici* Prevorčnik, Verovnik, Zagmajster & Sket, 2010	
	Monolistra (*Microlistra*) *pretneri* Sket, 1964	
	Monolistra (*Microlistra*) *pretneri pretneri* Sket, 1964	
	Monolistra (*Microlistra*) *pretneri spinulosa* Sket, 1965	
	Monolistra (*Monolistra*) *coeca intermedia* Sket, 1964	
	Monolistra (*Monolistra*) *monstruosa* Sket, 1970	
	Monolistra (*Monolistrella*) Sket, 1964	
	Monolistra (*Monolistrella*) *velkovrhi* Sket, 1960	
	Monolistra (*Pseudomonolistra*) *bosnica* Sket, 1970	
	Monolistra (*Pseudomonolistra*) *hercegovinensis atypica* Sket, 1965	
	Monolistra (*Pseudomonolistra*) *hercegovinensis brevipes* Sket, 1965	
	Monolistra (*Pseudomonolistra*) *radjai* Prevorčnik & Sket, 2007	
	Monolistra (*Typhlosphaeroma*) *bericum hadzii* Sket, 1959	
	Monolistra (*Typhlosphaeroma*) *matjasici* Sket, 1964	
	Monolistra (*Typhlosphaeroma*) *racovitzai conopyge* Sket, 1964	
	Monolistra (*Typhlosphaeroma*) *racovitzai karamani* Sket, 1959	
	Monolistra (*Typhlosphaeroma*) *racovitzai pseudoberica* Sket, 1964	
Stenasellidae	*Magniezia studiosorum* Sket, 1969	
Chordata		
Amphibia:Proteidae	*Proteus anguinus parkelj* Sket & Arntzen, 1994	
Teleostei: Nemacheilidae	*Triplophysa longibarbata* (Chen, Yang, Sket & Aljančič, 1998)	

Second, the intricate leech taxonomy was frustrating. As he stated in his interview with Traudl Krapp in Amphipoda Newsletters 40, the unsolved taxonomy of erpobdellid leeches motivated him to integrate molecular methodology into taxonomic expertise. In the mid 1990-ies he initiated Peter Trontelj's study visit to Tübingen, where he acquired training in molecular systematics. Upon return to Ljubljana, Peter established a molecular laboratory within the Boris' research team. Molecular phylogenies offered a new perspective on leech taxonomy. Some lineages, such as Erpobdellidae, emerged as well-supported monophyla (Trontelj et al. 1996). In a similar line, fine scale analyses confirmed species status of morphological forms within the *Glossiphonia complanata* species complex (Verovnik et al. 1999). More commonly, however, molecular phylogenetic structure deviated from traditionally accepted groupings and challenged higher taxa such as Rhynchobdellidae (Trontelj et al. 1999), or unveiled inadequate taxonomy in erpobdellid genera *Dina* and *Trocheta* (Trontelj and Sket 2000).

Crustacea: Decapoda

The cave shrimps of the genus *Troglocaris* are remarkable and common animals of the subterranean waters of the Dinaric Karst. Boris admired cave shrimps since he was a boy, but his contributions to knowledge about cave shrimps were mostly revisionary (but see Jugovic et al. 2019), confronting morphological and molecular variation of subterranean freshwater atyid shrimps in Europe. The molecular phylogeny of cave shrimps and surface atyids in Europe revealed unexpected phylogenetic relationships within the group, identified potential new species of cave shrimps and highlighted the necessity for taxonomic reassessment of the group (Zakšek et al. 2007). A comprehensive phylogeographic study of the species with holodinaric distribution pattern, i.e., *Troglocaris anopththalmus* species complex, showed that some large-ranged species are genetically deeply structured, possibly comprising several species (Trontelj et al. 2009; Zakšek et al. 2009). Under Boris' mentorship, PhD student Jure Jugovic utilized these phylogenetic insights to demonstrate that much of the morphological variation observed in cave shrimps is sex and age specific, that size alone is not indicative of an individual's age, and that adults represent the taxonomically most distinct stage in *Troglocaris* (Jugovic et al. 2010a). Furthermore, their research underscored that rostrum length, a traditionally important taxonomic character, is influenced by the presence of predatory olms, rendering it unreliable for species diagnosis (Jugovic et al. 2010b).

Using molecular phylogenies and reliable taxonomic characters, Boris and co-authors redefined the subgeneric structure of the genus *Troglocaris* (Sket and Zakšek 2009), described new species of cave shrimps (Sket and Zakšek 2009; Jugovic et al. 2011), as well as disentangled the species structure of the *Troglocaris anophthalmus* species complex (Jugovic et al. 2012).

Crustacea: Isopoda

Many of Boris' contributions to isopod taxonomy can be considered as footprints of his cave explorations around the globe, including Africa (Sket 1969), Bermuda (Sket

1979a), Sri Lanka (Sket 1982a), Mediterranean region (Sket 1990b), Philippines (Botosaneanu and Sket 1999), New Zealand (Sket and Bruce 2004) and Brazil (Prevorčnik et al. 2012). These expeditions yielded unexpected finds that contributed to global taxonomy of Asellota, Cymothida, Sphaeromatida and Calabozoa, with descriptions of new species, genera and families (e.g. (Sket 1985a).

Nevertheless, Boris' systematic isopod research primarily focused on groups inhabiting the Dinaric Karst and broader Mediterranean Region. He authored the very first revisions of the taxonomy and distribution of surface and subterranean populations of *Asellus aquaticus* (Sket 1963, 1965b, 1994a), an isopod that subsequently became a model for studying cave colonization, morphological differentiation and speciation. Other contributions addressed taxonomic status and occurrence of cirolanids and sphaeromatids in a broader Mediterranean region. Boris's contributions to the knowledge of the relatively few cirolanids of the region were mostly faunistic (Sket 1964a; Delić and Sket 2015), while his taxonomic endeavors focused on partial revisions of generic structures, renaming, and the description of new genera (Prevorčnik et al. 2016; Sket and Baratti 2021).

By contrast, the subterranean sphaeromatids are a common and speciose group, distributed along Dinaric Karst, southern slopes of Alps and Tyrrhenian coast on Apennine Peninsula. Boris laid foundations of taxonomy and biology of subterranean sphaeromatids of the genus *Monolistra* from the Dinaric region, dividing it into subgenera based on sexual size dimorphism, defensive spine structures and degree of reduction of the uropods (Sket 1964b, 1965a, 1982b, 1986e; Prevorčnik and Sket 2007; Prevorčnik et al. 2010).

The marine origin of subterranean sphaeromatids intrigued him deeply. Decades ago, he collected a posterior half of an unknown sphaeromatid in the anchihaline cave Šipun near the town of Cavtat (Croatia). This piece of an animal showed a morphology potentially transitional between a marine ancestor and its alleged descendants from subterranean freshwater (Sket 2012). It has become some sort of holy grail, and several lab members had the mission to complement their holidays at the Adriatic coast with a visit to Šipun Cave. Unfortunately, with no luck yet, so Boris passed away while the riddle still unsolved.

Although terrestrial isopods are common in caves, Boris never looked into their diversity. However, he did provide support for studies conducted by other authors on terrestrial isopods. Nonetheless, he compiled a checklist of this group (Sket 1986d).

Crustacea: Amphipoda

Amphipods were a particular passion of Boris (Fig. 3). He served in international consortia dedicated to compiling global amphipod checklists (Väinölä et al. 2008; Horton et al. 2023). A minor part of his taxonomic works can be associated with his expeditions, resulting in species descriptions from the families Bogidiellidae from China and Ecuador (Sket 1985c; Karaman and Sket 1990a); Sebidae from SE Asia (Jaume et al. 2009), Melitidae from Iran and Philippines (Sawicki et al. 2005; Krapp-Schickel and Sket 2015) and Pseudoniphargidae from Bermuda (Stock et al. 1987).

Figure 3. Left: The parkelj, or Krampus, from Boris' childhood memories, after which he named the black olm, *Proteus anguinus parkelj*. Right: Boris' favourite amphipods, *Niphargus balcanicus* (upper), and *Jugogammarus kusceri* (bottom). (Photo: Boris Sket archive).

More systematic research was devoted to two families, the predominantly subterranean Niphargidae and predominantly epigean Gammaridae s. lat. The genus *Niphargus* was the one that attracted his attention and some of his earliest papers are reports on Niphargidae (Sket 1956, 1958, 1960). His research of niphargid biology revolved around a few key topics. He described several species, subspecies and genera (Sket 1974, 1981b; Karaman and Sket 1989, 1990b; Sket 1990a; Sket and Karaman 1990; Sket 1999b; Fišer et al. 2006a, 2007a; Sket and Karaman 2018; Karaman and Sket 2019). To contribute towards the complex taxonomy of the family, he trained his PhD student, Cene Fišer. Boris had an excellent overview of the niphargid morphological variation, including changes of morphology during development (Sket 1974; Fišer et al. 2008b). He dearly hoped that the high number of species within genus *Niphargus* could be classified into a few phylogenetically supported subgenera. To this end, he conducted several revisions with in-depth discussions on individual characters (Sket 1971, 1972), followed by a few partial cladistic revisions (Sket and Notenboom 1993; Fišer et al. 2006b, 2010) and pioneering attempts of web-based morphological taxonomy that were ahead of their time (Fišer et al. 2009b, 2009a). The first molecular phylogenies, however, revealed a repeated evolution of multiple convergences, with no reliable characters that could satisfactorily diagnose subgenera (Fišer et al. 2008a; Trontelj et al. 2009).

His interest in Gammaridae s. lat. manifested relatively late and was closely tied to his passion for the fauna of ancient freshwater lakes. His vivid interest for ancient lakes resulted in the descriptions of species from the gammaridean family Anisogammaridae from the Chinese lake Fuxian Hu (Sket 2000; Sket and Fišer 2009). An important breakthrough in gammaridean research was a global phylogenetic analysis of the Gammaridae s. lat., conducted in collaboration with Chinese researches. In this study was shown that gammarids colonized freshwater multiple times and subsequently diversified in it (Hou et al. 2011), yet diversification patterns of different lineages varied between evolutionary stasis and rapid diversifications corresponding to adaptive radiations (Hou et al. 2014). These influential studies fully exposed the extent of the taxonomic complexity of Gammaridae s. lat., which encompass several morphological distinct yet phylogenetically non-justified families and genera (Hou and Sket 2015; Sket and Hou 2018b). The phylogenetic framework prompted several attempts to revise the taxonomic structure of the family (Hou and Sket 2015; Sket and Hou 2018a), as well as discussions on taxonomic status of several species complexes (Mamos et al. 2014; Sidorov et al. 2018; Sket et al. 2019; Hou et al. 2022).

Other taxa

The Dinaric stygofauna is renowned for its exotics, which include suspension feeders like sponges, subterranean hydroids, clams, tube worms, and notably, the olm, the only European subterranean amphibian. Boris made significant contributions to the taxonomy and overall understanding of all these species.

Boris described the first troglobitic sponge, *Eunapius subterraneanus*, which was later primarily studied by his teaching assistant, Milan Velikonja. Together, they compiled an overview of the distribution and taxonomic status of both obligate and non-obligate subterranean sponges (Sket and Velikonja 1986).

The only Dinaric subterranean hydrozoan was discovered accidentally in preserved samples. This weird animal was initially noticed by Boris' technical assistant, France Velkovrh. When he reported his finding to Boris and their superior, Prof. Janez Matjašič, his report was met with disbelief. Subsequent examinations confirmed the presence of the subterranean species in the Rak Channel of the Planinska jama (Postojna Planina cave system). In recognition of France Velkovrh's contribution, the enigmatic cnidarian was named as *Velkovrhia enigmatica* (Matjašič and Sket 1971).

Although Boris was not the primary describer, his work played a crucial role in the recognition of the unique subterranean clam *Congeria kusceri*. The species was described in 1962 by Professor Jože Bole. At that time, malacologists considered *Congeria* to be an extinct genus, known only from diverse and widespread fossil records. The original description of the species was in Slovene, which led to it being overlooked internationally. The collaboration with Brian Morton resulted in a systematic revision of morphology and extensive review of the biology of this living fossil (Morton et al. 1998). Later on, Boris challenged the validity of its classification within the genus *Congeria*, and proposed it be reclassified under the extant genus *Mytilopsis* (Sket 2011). This proposal, however, received little attention and is not consistent with molecular phylogeny.

Boris made significant contributions to our understanding of the natural history of the olm through several influential papers. Most notably, he described the non-troglomorphic form discovered in the late 1980s in Bela Krajina, naming it *Proteus anguinus parkelj* (Sket and Arntzen 1994; Arntzen and Sket 1996, 1997). The discovery of the black proteus was a major surprise, and Boris openly admitted that he "envied Andrej Mihevc who actually caught the first specimen." The description was augmented by allozyme polymorphism data, which was the standard molecular taxonomic tool of that time. Based on distributional evidence, Boris hypothesized that i) the olm was a recent, post-Pleistocene colonizer of caves, ii) which colonized caves in several colonization events, from iii) the ancestral surface populations that were already genetically differentiated, and iv) that subterranean populations convergently evolved a similar morphological phenotype (Sket 1997).

Finally, his curiosity extended beyond the metazoan life: he encouraged the first explorations of the microbial composition of the "cave gold" in Slovenia (Megušar and Sket 1977). Recognizing the importance of biofilm, he kept eyes open to pursue this topic. His patience was paid-off decades later, with two studies. The first follow up of the early explorations of cave gold revealed a completely unknown bacterial flora in the Slovenian cave Pajsarca (Pašić et al. 2010). The second study meticulously explored the physical and biological structure of a sprout-like biofilm from Vjetrenica, uncovering a diverse microbial flora and the complex physical structure of cortex and medulla of these sprouts (Kostanjšek et al. 2013).

The origin and evolution of subterranean fauna

The question of the origin of subterranean organisms was a recurring theme in Boris' discussions, albeit in various contexts. He viewed evolution as a fundamental aspect of the scientific work in speleobiology. His primary questions regarding most speleobiological phenomena were "how or why did it develop, why did it happen—to be different from the epigean?"

The origin of subterranean organisms was a topic of lively debate in the 1970s and the 1980s. Researchers recognized the relatedness between subterranean aquatic organisms and both freshwater and marine faunas, suggesting its dual origin. Boris hypothesized that Dinaric subterranean aquatic fauna derived i) directly from marine ancestors, ii) directly from the freshwater ancestors, and iii) from marine ancestors via transitionary surface freshwater phase. He inferred the epigean ancestry of Dinaric subterranean fauna based on his observations of global species distributions. The olm as an amphibian, clearly derived from freshwater species (Sket 1997). Likewise, the origin of subterranean water lice (*Asellus aquaticus*) or *Synurella ambulans* in presence of surface populations was not in question. The cave tube worm (*Marifugia cavatica*) is a marine element, that presumably colonized freshwater through anchialine caves or submerged springs. This hypothesis was consistent with molecular phylogeny indicating that the close relatives of the cave tube worm are *Ficopomatus* living also in the Adriatic Sea. Importantly, *Ficopomatus* species live in a wide range of salinities, from fully marine to

brackish waters (Kupriyanova et al. 2009). An intriguing case presented subterranean sphaeromatid isopods. Sphaeromatidae are predominantly a marine crustacean family. However, Boris noted that the distribution of some species followed the boundaries of paleodrainage basins, leading him to assume that marine species initially colonized surface freshwater, dispersed, and speciated in the surface realm before subsequently colonizing the subterranean realm (Sket 1986b).

Boris argued that subterranean realm was colonized independently on different occasions, refereeing, for example, to morphology and distribution of water lice and olm (Sket 1994a, 1997; Turk et al. 1996). This hypothesis was supported later by molecular phylogenies (Verovnik et al. 2004). He suggested that the varying degrees of morphological similarity between subterranean organisms (in comparison to surface ancestors) resulted from convergent evolution during cave colonization (Sket 1985c, 1997; Turk et al. 1996). Generally, Boris was critical of comparisons between distantly related surface and subterranean species, advocating for model systems comprising closely related species, ideally sister pairs (Simčič and Sket 2019, 2021). To this end, he encouraged research on *Asellus aquaticus*. The efforts of his PhD students and close associates, Simona Prevorčnik, Rudi Verovnik and Peter Trontelj, resulted in Europe-wide phylogeography and extensive morphometrics of water lice providing the evidence that i) Dinaric region acted as a refugium during Pleistocene glaciations, ii) most subterranean populations are genetically completely isolated from adjacent surface populations despite occasional contact, and iii) water lice colonized caves on several occasions relatively recently (Sket 1994a; Verovnik et al. 2003, 2004, 2005). Morphological analyses revealed a rather uniform morphology of surface populations (Prevorčnik et al. 2009), while subterranean populations showed substantial differences from surface ones, including the lack of eyes and pigment. Nevertheless, subterranean populations varied among different caves, suggesting imperfect convergence due to differences among subterranean habitats (Turk et al. 1996; Sket 1997; Prevorčnik et al. 2004).

Boris vividly disagreed with many peers who hypothesized that cave animals no longer evolve. He supported his claims with evidence from various cases, including species living in cave hygropetric environments and *Niphargus* amphipods. Cave hygropetric is a habitat of a permanent weaker or stronger current flowing along the vertical cave rock. Boris became aware of this peculiar subterranean habitat when he noted that some species were regularly found in it (Sket 2004). Despite being unrelated, e.g., beetles and amphipod crustaceans, these species shared characters such as prehensile claws and filter-like mouthparts. This similarity suggests that cave hygropetric is a distinct habitat within the subterranean environment, and some specialized subterranean inhabitants exploit its resources (Sket 2004). A different, yet compatible line of reasoning was used to explain the enormous morphological variation in the amphipod genus *Niphargus*. Boris suggested that *Niphargus* variation in morphology could be associated with ecological differentiation (Sket 1999a). Phylogenetic analyses suggested that much of this variation cannot be attributed to cladogenetic events alone (Fišer et al. 2008a). Many morphologically similar species evolved multiple times (Trontelj et al. 2009). These cases of convergence within entire subterranean clades indicated that the vague term "subterranean environment" comprises replicated subterranean habi-

tats with similar selection pressures, and ongoing evolution within the subterranean realm. The proximal mechanism driving morphological variation could be attributed to heterochrony (Fišer et al. 2008b).

Biodiversity patterns and biogeography

Since his early career, Boris paid attention to data collection and data management. His systematic collection of species distributions in the Western Balkans predated the computer era. The very first records were kept in registers on data-cardboards. These were later digitized in MS Word and MS Excel files. The systematic storage using relational databases began when Maja Zagmajster enrolled in her PhD program, resulting in the development of the SubBioDB database (Zagmajster et al. 2012).

Boris was deeply interested in biogeographical and biodiversity patterns at different scales, asking, for example, where the areas with the highest numbers of troglobionts are, what the general biodiversity patterns are, how much these patterns can be trusted, and which factors shaped them. He advocated that species richness needs to be corrected by the size of a region, and demonstrated that the Dinaric Karst was a global hotspot in subterranean species richness. In studies of biodiversity patterns, he served as both a collaborator and a primary investigator. His biogeographic opus revolved around the distribution of species-rich caves and regions, and biodiversity patterns within the Dinaric Karst.

Species-rich caves and species-rich regions

In 2000, David Culver and Boris Sket published one of the most influential papers in subterranean biology, addressing a straightforward question: how many "species-rich" caves, each counting 20 or more troglobionts are there, and where in the world they are (Culver and Sket 2000). By introducing the arbitrarily defined measure of "richness" or "hotspot," this paper enabled the scaling of any faunistic list and established a comparative framework for studying species richness in individual caves. It marked a milestone in the exploration of subterranean hotspots and patterns of subterranean biodiversity. Noteworthy, the paper already indicated that most of species-rich caves are located outside the tropics, at mid-latitudes.

Data from Slovenian caves facilitated further pioneering spatial studies led by David Culver. An analysis of Slovenian subterranean species richness showed that the spatial position of hotspots was stable and could be predicted from the position of species-rich caves, that the species composition of the region is far from complete (Culver et al. 2004a) and that the length of cave passages, their altitude and depth may predict terrestrial species richness (Culver et al. 2004b). These regional studies grounded considerations of the first global analysis that eventually resulted in another influential hypothesis of "mid-latitude ridge of high subterranean species richness", stating that the regions with the highest numbers of species were aligned along mid-latitudes, presumably reflecting the availability of habitat and high productivity on a surface (Culver et al. 2006).

Dinaric Karst as a global hotspot in subterranean biodiversity

Spatial representations of the collected data on the map of the Western Balkans brought Boris to three main findings.

First, the patterns of subterranean terrestrial and aquatic fauna differ. While terrestrial species richness peaks in the NW and SE, aquatic species richness is highest in the NW (Sket 1994b; Sket et al. 2004a). Detailed analyses decades later corroborated this observation, even after taking into account the spatial extent of analysis and sampling bias (Zagmajster et al. 2008, 2010; Bregović et al. 2019).

Second, Boris recognized that subterranean taxa in the Western Balkans can be classified into five major biogeographic groups (Sket 1994b). Some taxa, such as the olm, cave shrimp and tube worm had holodinaric distribution, spanning from the northwest margins of the Dinaric Karst to the political border between Herzegovina and Montenegro for *Proteus* and *Marifugia*, and even beyond for *Troglocaris*. This distribution was subsequently confirmed in later studies, although recent research acknowledges that these patterns pertain to the genus or species complex level (Sket 1997; Fišer et al. 2007a; Zakšek et al. 2009). Other groups of taxa were found to inhabit smaller areas within the Dinaric Karst, displaying a merodinaric distribution, which encompassed the northwest, southeast, epi-, and paralittoral compartments of the Dinaric Karst. Apart from these, Dinaric Karst inhabit also transdinaric species, which extend their distributional ranges beyond the Dinaric Karst, either in southern Europe or in the southeastern Mediterranean region (Sket 1994b).

Third, Boris hypothesized that distribution patterns are primarily associated with geological history, whereas recent ecological conditions and dispersal play only minor roles. He observed that some species distributions follow paleo-drainages rather than recent ones (Sket 1986b, 2002). He assumed that distributional patterns of the subterranean species were often shaped already on the surface, prior the surface ancestor in multiple colonization events evolved into subterranean descendant (Sket 1994b). By comparing distributional patterns of surface and subterranean relatives, he suggested that distribution of Dinaric subterranean species should be associated with disjunct karstification centers of the Dinaric Karst, the extent of the Pannonian Sea and drying up of the Paratethys, the Messinian Crisis, and Pleistocene glaciations (Sket 1981a, 1988, 1994b). Calibrated molecular phylogenies subsequently provided additional evidence that much of the Dinaric fauna pre-dated the Pleistocene (Trontelj et al. 2007).

On a local scale, Boris acknowledged the significance of ecological dynamics, which emerged as an interplay between interspecific competition and ecological specialization. His analyses of fauna associated with anchialine caves (Sket 1977, 1986a) and thermal water (Sket and Velkovrh 1981a) provided indirect evidence that physical and chemical properties of water could deterministically shape species distribution. In many papers he assumed a covariation between the degree of species ecological specialization and species competitive strength, resulting in outcompeting weaker generalists bymore specialized species (Sket 1981a, 1986a). He never doubted the role of interspecific relationships and used it as a *post hoc* explanation for distribution of many species (Sket 1986a), as a

mechanism for maintaining allopatric distributions (Sket 1994b) and as a possible driver of the colonization of the subterranean realm (Sket 1981a, 2002). His later research showed that the outcome of the interspecific relationship between surface and subterranean species might be less predictable than previously thought (Fišer et al. 2007b).

Ecology

The properties of subterranean environment such as darkness, oligotrophy and stable conditions have rendered ecology an inevitable part of subterranean biology. Understanding the diversity of ecological factors within the subterranean realm was probably pivotal for Boris' views on imperfect convergent evolution (previous section), and also shaped his opinion on threats to subterranean ecosystem. Boris examined the interaction between organism and its environment from two aspects.

The old question, how to treat species found in a cave, Boris addressed theoretically (Sket 2008b). In his review, he was seeking for the simplest compromise among existing classifications of cave organisms, and proposed criteria for their delimitation based on the ecology of species' life cycles. An essential takeaway from his own observations was the necessity for rigorous testing to determine the ecological status of a species, emphasizing that conclusions should not be based solely on superficial impressions. He highlighted that troglobionts may not necessarily exhibit troglomorphism, and conversely, surface-dwelling animals can lack eyes.

In addition, Boris studied the variation of ecological conditions within the subterranean ecosystems in conjunction with community composition. He significantly advanced our understanding of sinking streams, anchihaline caves, fissure systems, and cave hygropetric. Sinking streams were explored in Postojna-Planina cave system between 1965–76 (Sket 1970, 1979b; Sket and Velkovrh 1981b). Sket and collaborators regularly monitored 16 sampling sites along the Pivka River. They measured annual variation in temperature, oxygen, nitrates and bacterial oxygen consumption, as well as community structure. Apart from the updated checklist of the system and vicinity (Sket 1979b), they showed daily and annual temperature fluctuations, gradually declining in dependence of distance from sink and water volume, i.e. the impact from the surface penetrated deeper into cave system at high water level and strong currents. Moreover, they showed that water during its flow through the cave gets oxygenated, whereas nitrogen wastes remain intact (Sket 1970). These studies were a basis for a Slovenian-Brazilian bilateral project 50 years later, with the aim of geographically broadening the study system and evaluating the impact of decades of anthropogenic activities on subterranean biota. Boris was the leader of the Slovenian team, the results still pending the final publication.

As a part of his investigation of the Postojna-Planina cave system, Boris paid focused on water drips. In collaboration with Anton Brancelj and Cvetka Žagar, they showed that these waters harbor unique communities, primarily dominated by copepod crustaceans (Sket 1981b; Sket et al. 2004b). The study allowed the discovery of

a point endemic, *Niphargobates orophobata*, found in a single jet of percolating water. Their findings underscored the exceptional nature of the fauna inhabiting percolated water and significantly contributed to our understanding of epikarst and water-filled fissure systems (Sket 1981b).

Boris conducted pioneering research on the ecology of anchihaline caves globally, focusing on several caves along the Adriatic coast (Sket 1986a, 1996b) (Fig. 4). Water chemistry measurements clearly showed three layers of water: bottom marine, uppermost freshwater and an intermediate, thin layer of halocline with depleted oxygen and rapid transition from poly- to oligohaline conditions. Each of these layers comprised unique ecological habitat, each supporting its own fauna. Using comparative data, Boris elegantly demonstrated that species vertical distribution within the anchihaline water column reflected the interplay between species needs for abiotic environment and interspecific interactions. For example, the amphipod *Niphargus hebereri*, predominantly found in fresh- and only rarely in brackish water, preferred freshwater layer despite its tolerance for mesohaline water; its distribution mostly reflected species' habitat choice. By contrast, the thermosbenacean *Monodella halophila* was found in a presumably predation-free zone within the halocline layer, although it lives in freshwater. The distribution of this species was indicative of its generalistic nature and weak competitiveness (Sket 1986a, 1996b).

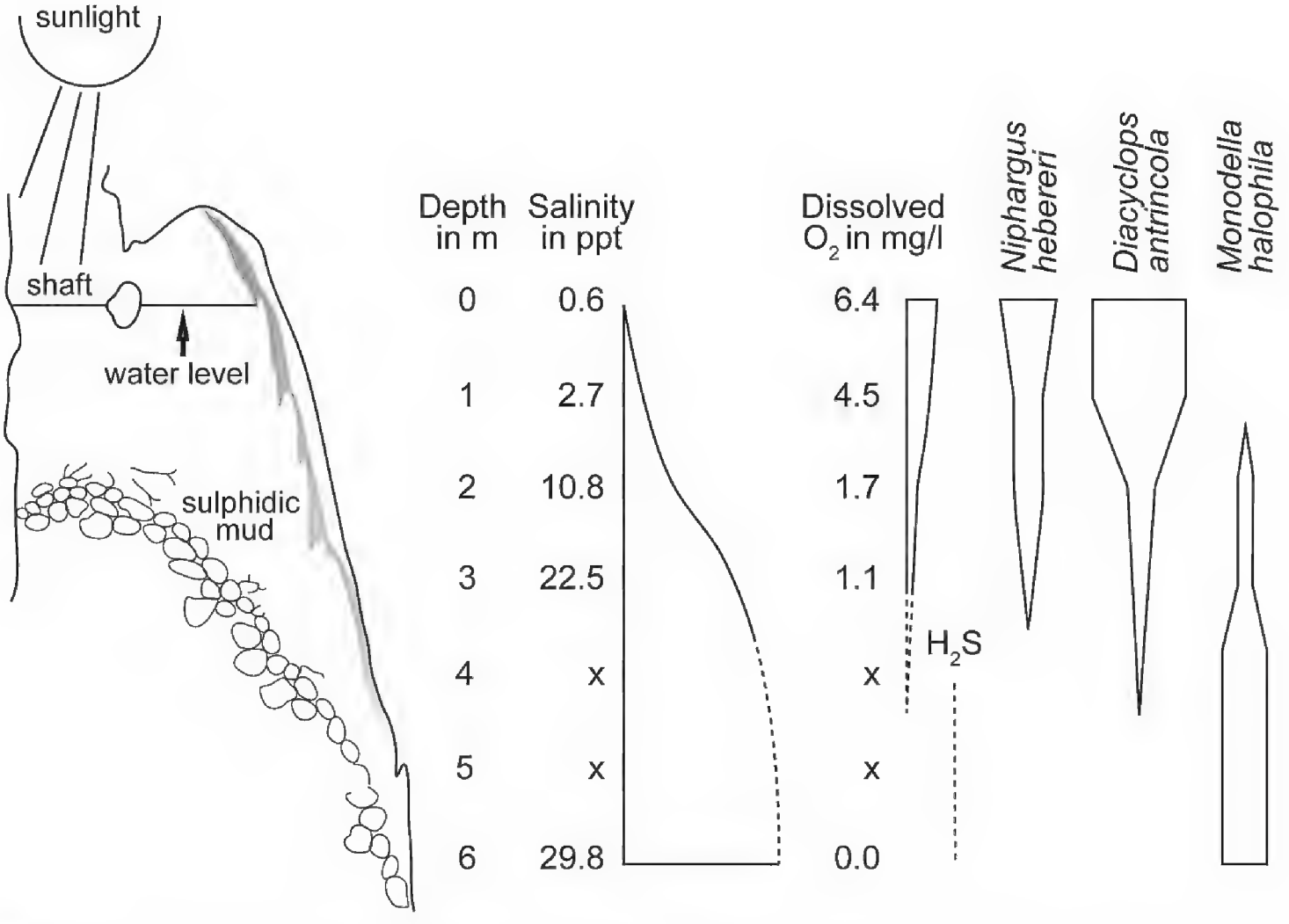

Figure 4. Ecological stratification of water column in anchialine caves. Boris was one the first who studied the vertical stratification of abiotic factors and with it associated community structure. After Sket 1896.

Conservation biology

Boris advocated that subterranean fauna comprises an important part of global and Slovenian natural heritage. His analyses of Slovenian subterranean fauna revealed that the proportion of subterranean species in Slovenia surpassed that found on a global scale (Sket 1999a, 1999c). An important part of his research was devoted to recognition of threats and processes that could aid in the protection of subterranean natural heritage.

He early realized that cave fauna is threatened by the anthropogenic disturbance originating at the surface. One of his early notifications was that of organic pollution in the subterranean flow of the Pivka River in the Postojna-Planina Cave system. This pollution led to an influx of immigrants from the surface and the subsequent disappearance of specialized subterranean species. Boris presumed that eutrophication weakened surface-subterranean barrier resulting in altered community structure and increased interspecific competition pressure on subterranean species (Sket 1970).

Most of subterranean species are endemic (Bole et al. 1993). This view was further rectified by systematic analyses conducted within the European project PASCALIS (Deharveng et al. 2009). Many species live only in small areas, and subterranean communities are characterized by a high beta diversity (Malard et al. 2009), leading to high global (gamma) diversity. Species with large distribution ranges - i.e., larger than 200 km - are often taxonomic artifacts (Trontelj et al. 2009). Boris argued that endemicity, in conjunction with K-strategies, makes subterranean fauna vulnerable (Sket 1999a, 1999c).

To actively contribute to the protection of subterranean fauna, Boris undertook several initiatives. He prepared a series of checklists (Sket 1986f; Sket et al. 1991, 2004a) and conducted assessments of the endangerment status for various species in Slovenia, including leeches (Sket 1992c, 1996a), crustaceans (Sket 1992d; Sket and Brancelj 1992), amphibians (Sket 1992e), and the other species from groundwater (Sket 1992f). Together with David Culver, Boris provided recommendations for the monitoring of caves, advocating for the standardization of sampling effort using fixed time-person units, as well as the use of baiting of terrestrial pitfall traps and aquatic traps, as well as the potential utilization of the capture-mark-recapture method, with a caution note that an increase of population size may indicate eutrophication (Culver and Sket 2002). He also developed criteria and provided a list of caves as habitat type "caves not open to the public" of the Annex II of the Habitat's Directive, that are part of Natura 2000 network in Slovenia.

Several efforts were made to safeguard species-rich caves (Sket 1992a) and/or regions (Michel et al. 2009). Boris had ambitious plans that aimed to establish a network of species-rich regions along the Dinaric Karst, ultimately seeking UNESCO protection. Unfortunately, these efforts were in vain. Boris firmly believed that protecting Slovenian rich-natural heritage is our moral imperative. The message he frequently reiterated was "There is no reason to be proud of our natural heritage, as long the Pivka River draining through the global subterranean hotspot of Postojna-Planinska Cave system, remains polluted".

Figure 5. Field work. (Photo: Boris Sket archive).

The outreach

Boris stood out as one of the most prominent and influential zoologists in Slovenia. As a professor at the University of Ljubljana, he played a pivotal role in shaping the education of numerous generations of biology students and teachers. While teaching courses such as Invertebrate Zoology and Evolution, he also introduced the subject of "Subterranean Biology" into the biology curriculum. Under his mentorship, ten PhD students, five MSc students, and 25 graduate students successfully completed their studies. Many of these individuals have become respected zoologists in various research fields. Among these, we must mention Milan Velikonja, who studied subterranean sponges, Anton Brancelj, who established the model of epikarst and became one of the world-leading taxonomists for microcrustaceans, Tone Novak, who studied cave fauna outside Dinaric Karst with an emphasis on opilionid taxonomy and physiological adaptations, and the research team SubBioLab.

Beyond his teaching and research endeavors, he also paid attention to broader audience interested in natural sciences. He regularly contributed to the popular science magazine "Proteus," sharing his insights and knowledge with a wider readership. Furthermore, in the 1970s, he edited a series of identification keys for various groups of animals, making valuable information accessible to enthusiasts and researchers alike. Together with Meta Povž, he co-authored a comprehensive book on Slovenian fishes in 1990. This impressive

volume detailed the Slovenian fish fauna, providing descriptions and insights into the biology of various species. Moreover, Boris was a writer and co-editor of the expansive monograph "Živalstvo Slovenije" (The Fauna of Slovenia). This exhaustive volume presented Slovenian fauna in an accessible and comprehensive manner, covering anatomy, ecology, and diversity, catering to students and naturalists alike. Lastly, he authored a high school textbook on Evolution, further contributing to science education at various levels.

Boris influence extended beyond the biological and naturalist communities. Through his writings in daily newspapers, he persistently advocated for the protection of our natural heritage, with a voice of a man who eyewitnessed the transformation of society and environmental degradation. He was one of the giants, whose shoulders allow us seeing further.

References

Arntzen JW, Sket B (1996) Speak of the devil: the taxonomic status of *Proteus anguinus parkelj* revisited (Caudata: Proteidae). Herpetozoa 8: 165–166.

Arntzen JW, Sket B (1997) Morphometric analysis of black and white European cave salamanders, *Proteus anguinus*. Journal of Zoology 241: 699–707. https://doi.org/10.1111/j.1469-7998.1997.tb05742.x

Bole J, Drovenik B, Mršić N, Sket B (1993) Endemic animals in hypogean habitats in Slovenia. Naše jame : glasilo Jamarske zveze Slovenije 35: 43–55.

Botosaneanu L, Sket B (1999) A new freshwater stygobiotic species of *Cyathura* (Isopoda: Anthuridae) from Bohol Island, the Philippines. Acta Biologica Slovenica 42: 27–33.

Bregović P, Fišer C, Zagmajster M (2019) Contribution of rare and common species to subterranean species richness patterns. Ecology and Evolution 9: 11606–11618. https://doi.org/10.1002/ece3.5604

Chevaldonné P, Sket B, Marschal C, Lejeusne C, Calado R (2008) Improvements to the "Sket bottle": A simple manual device for sampling small crustaceans from marine caves and other cryptic habitats. Journal of Crustacean Biology 28: 185–188. https://doi.org/10.1651/07-2923R.1

Culver DC, Christman MC, Sket B, Trontelj P (2004a) Sampling adequacy in an extreme environment: Species richness patterns in Slovenian caves. Biodiversity and Conservation 13: 1209–1229. https://doi.org/10.1023/B:BIOC.0000018153.49280.89

Culver DC, Christman MC, Šereg I, Trontelj P, Sket B (2004b) The Location of Terrestrial Species-Rich Caves in a Cave-Rich Area. Subterranean Biology 2: 27–32.

Culver DC, Deharveng L, Bedos A, Lewis JJ, Madden M, Reddell JR, Sket B, Trontelj P, White D (2006) The mid-latitude biodiversity ridge in terrestrial cave fauna. Ecography 29: 120–128. https://doi.org/10.1111/j.2005.0906-7590.04435.x

Culver DC, Sket B (2000) Hotspots of subterranean biodiversity in caves and wells. Journal of Cave and Karst Studies 62: 11–17.

Culver DC, Sket B (2002) Biological monitoring in caves (Biološko zasledovanje stanja (monitoring) v jamah. Acta Carsologica 31: 55–64. https://doi.org/10.3986/ac.v31i1.403

Deharveng L, Stoch F, Gibert J, Bedos A, Galassi D, Zagmajster M, Brancelj A, Camacho A, Fiers F, Martin P, Giani N, Magniez G, Marmonier P (2009) Groundwater biodiversity in Europe. Freshwater Biology 54: 709–726. https://doi.org/10.1111/j.1365-2427.2008.01972.x

Delić T, Sket B (2015) Found after 60 years : the hows and whys of *Sphaeromides virei montenigrina* (Crustacea : Isopoda : Cirolanidae) rediscovery in Obodska pećina , Montenegro. Natura Sloveniae 17: 59–65. https://doi.org/10.14720/ns.17.2.59-65

Fišer C, Bininda-Emonds ORP, Blejec A, Sket B (2008b) Can heterochrony help explain the high morphological diversity within the genus *Niphargus* (Crustacea: Amphipoda)? Organisms Diversity and Evolution 8: 146–162. https://doi.org/10.1016/j.ode.2007.06.002

Fišer C, Coleman CO, Zagmajster M, Zwittnig B, Gerecke R, Sket B (2010) Old museum samples and recent taxonomy: A taxonomic, biogeographic and conservation perspective of the *Niphargus* tatrensis species complex (Crustacea: Amphipoda). Organisms Diversity & Evolution 10: 5–22. https://doi.org/10.1007/s13127-010-0006-2

Fišer C, Keber R, Kereži V, Moškrič A, Palandančić A, Petkovska V, Potočnik H, Sket B (2007b) Coexistence of species of two amphipod genera: *Niphargus timavi* (Niphargidae) and *Gammarus fossarum* (Gammaridae). Journal of Natural History 41: 2641–2651. https://doi.org/10.1080/00222930701661225

Fišer C, Sket B, Stoch F (2006a) Distribution of four narrowly endemic *Niphargus* species (Crustacea: Amphipoda) in the western Dinaric region with description of a new species. Zoologischer Anzeiger 245: 77–94. https://doi.org/10.1016/j.jcz.2006.05.003

Fišer C, Sket B, Trontelj P (2008a) A phylogenetic perspective on 160 years of troubled taxonomy of *Niphargus* (Crustacea: Amphipoda). Zoologica Scripta 37: 665–680. https://doi.org/10.1111/j.1463-6409.2008.00347.x

Fišer C, Sket B, Turjak M, Trontelj P (2009a) Public online databases as a tool of collaborative taxonomy: A case study on subterranean amphipods. Zootaxa 56: 47–56. https://doi.org/10.11646/zootaxa.2095.1.5

Fišer C, Trontelj P, Sket B (2006b) Phylogenetic analysis of the *Niphargus orcinus* species–aggregate (Crustacea: Amphipoda: Niphargidae) with description of new taxa. Journal of Natural History 40: 2265–2315. https://doi.org/10.1080/00222930601086572

Fišer C, Trontelj P, Luštrik R, Sket B (2009b) Toward a unified taxonomy of *Niphargus* (Crustacea: Amphipoda): a review of morphological variability. Zootaxa 2061: 1–22. https://doi.org/10.11646/zootaxa.2061.1.1

Fišer C, Zakšek V, Zagmajster M, Sket B (2007a) Taxonomy and biogeography of *Niphargus steueri* (Crustacea: Amphipoda). Limnology 8: 297–309. https://doi.org/10.1007/s10201-007-0221-5

Horton T, De Broyer C, Bellan-Santini D, Coleman CO, Copilaș-Ciocianu D, Corbari L, Daneliya ME, Dauvin J-C, Decock W, Fanini L, Fišer C, Gasca R, Grabowski M, Guerra-García JM, Hendrycks EA, Hughes LE, Jaume D, Kim Y, King RA, Brutto S Lo, Lörz, A-N, Mamos T, Serejo CS, Senna AR, Souza-Filho JF, Tandberg AHS, Thurston MH, Vader W, Väinölä R, Domedel GV, Vandepitte L, Vanhoorne B, Vonk R, White KN, Zeidler W (2023) The World Amphipoda Database: History and Progress. Records of the Australian Museum 75: 329–342. https://doi.org/10.3853/j.2201-4349.75.2023.1875

Hou Z, Jin P, Liu H, Qiao H, Sket B, Cannizzaro AG, Berg DJ, Li S (2022) Past climate cooling promoted global dispersal of amphipods from Tian Shan montane lakes to circumboreal lakes. Global Change Biology 28: 3830–3845. https://doi.org/10.1111/gcb.16160

Hou Z, Sket B (2015) A review of Gammaridae (Crustacea: Amphipoda): the family extent, its evolutionary history, and taxonomic redefinition of genera. Zoological Journal of the Linnean Society 176(2): 323–348. https://doi.org/10.1111/zoj.12318

Hou Z, Sket B, Fišer C, Li S (2011) Eocene habitat shift from saline to freshwater promoted Tethyan amphipod diversification. Proceedings of the National Academy of Sciences of the United States of America 108: 14533–14538. https://doi.org/10.1073/pnas.1104636108

Hou Z, Sket B, Li S (2014) Phylogenetic analyses of Gammaridae crustacean reveal different diversification patterns among sister lineages in the Tethyan region. Cladistics 30: 352–365. https://doi.org/10.1111/cla.12055

Jaume D, Sket B, Boxshall GA (2009) New subterranean Sebidae (Crustacea, Amphipoda, Gammaridea) from Vietnam and SW Pacific. Zoosystema 31: 249–277. https://doi.org/10.5252/z2009n2a3

Jugovic J, Jalžić B, Prevorčnik S, Sket B (2012) Cave shrimps *Troglocaris* s. str. (Dormitzer, 1853), taxonomic revision and description of new taxa after phylogenetic and morphometric studies. Zootaxa 3421: 1–31. https://doi.org/10.11646/zootaxa.3421.1.1

Jugovic J, Prevorčnik S, Aljančič G, Sket B (2010b) The atyid shrimp (Crustacea: Decapoda: Atyidae) rostrum: phylogeny versus adaptation, taxonomy versus trophic ecology. Journal of Natural History 44: 2509–2533. https://doi.org/10.1080/00222933.2010.502258

Jugovic J, Prevorčnik S, Blejec A, Sket B (2011) Morphological differentiation in the cave shrimps *Troglocaris* (Crustacea: Decapoda: Atyidae) of the Dinaric karst - a consequence of geographical isolation or adaptation? Journal of Zoological Systematics and Evolutionary Research 49: 185–195. https://doi.org/10.1111/j.1439-0469.2010.00611.x

Jugovic J, Prevorčnik S, Sket B (2010a) Development of sexual characters in the cave shrimp genus *Troglocaris* (Crustacea: Decapoda: Atyidae) and their applicability in taxonomy. Zootaxa 2488: 1–21. https://doi.org/10.11646/zootaxa.2488.1.1

Jugovic J, Zakšek V, Petković M, Sket B (2019) A shrimp out of place. New genus of Atyidae (Crustacea: Decapoda) in subterranean waters of southeastern Europe, with some remarks on Atyidae taxonomy. Zoologischer Anzeiger 283: 111–123. https://doi.org/10.1016/j.jcz.2019.08.007

Karaman GS, Sket B (1989) *Niphargus* species (Crustacea: Amphipoda) of the Kvarner-Velebit Islands (NW Adriatic, Yugoslavia). Biološki vestnik 37: 19–36.

Karaman GS, Sket B (1990a) *Bogidiella sinica* sp. n. (Crustacea: Amphipoda) from southern China. Biološki vestnik 38: 35–48.

Karaman GS, Sket B (1990b) Two new *Niphargus* species (Amphipoda) from caves in Yugoslavia. International Journal of Speleology 19: 51–66. https://doi.org/10.5038/1827-806X.19.1.5

Karaman GS, Sket B (2019) New genus and species of the family Niphargidae (Crustacea: Amphipoda: Senticaudata), *Chaetoniphargus lubuskensis* gen. nov., sp. nov. from Croatia. Zootaxa 4545: 249–263. https://doi.org/10.11646/zootaxa.4545.2.5

Kostanjšek R, Pašić L, Daims H, Sket B (2013) Structure and Community Composition of Sprout-Like Bacterial Aggregates in a Dinaric Karst Subterranean Stream. Microbial Ecology 66: 5–18. https://doi.org/10.1007/s00248-012-0172-1

Krapp-Schickel T, Sket B (2015) *Melita mirzajanii* n. sp. (Crustacea: Amphipoda: Melitidae), a puzzling new member of the Caspian fauna. Zootaxa 3948: 248–262. https://doi.org/10.11646/zootaxa.3948.2.6

Kupriyanova EK, Ten Hove HA, Sket B, Zakšek V, Trontelj P, Rouse GW (2009) Evolution of the unique freshwater cave-dwelling tube worm *Marifugia cavatica* (Annelida: Serpulidae). Systematics and Biodiversity 7: 389–401. https://doi.org/10.1017/S1477200009990168

Malard F, Boutin C, Camacho AI, Ferreira D, Michel G, Sket B, Stoch F (2009) Diversity patterns of stygobiotic crustaceans across multiple spatial scales in Europe. Freshwater Biology 54: 756–776. https://doi.org/10.1111/j.1365-2427.2009.02180.x

Mamos T, Wattier R, Majda A, Sket B, Grabowski M (2014) Morphological vs. molecular delineation of taxa across montane regions in Europe: the case study of *Gammarus balcanicus* Schäferna, (Crustacea: Amphipoda). Journal of Zoological Systematics and Evolutionary Research 52: 237–248. https://doi.org/10.1111/jzs.12062

Matjašič J, Sket B (1971) Jamski hidroid s slovenskega krasa. Biološki vestnik 19: 139–145.

Megušar F, Sket B (1977) On the nature of some organic covers on the cave-walls. In: Panoš V (Ed.) Proceedings of the 6th international congress of speleology. Olomuc, ČSSR, 159–161.

Michel G, Malard F, Deharveng L, Di Lorenzo T, Sket B, De Broyer C (2009) Reserve selection for conserving groundwater biodiversity. Freshwater Biology 54: 861–876. https://doi.org/10.1111/j.1365-2427.2009.02192.x

Minelli A, Sket B, de Jong Y (2014) Fauna Europaea: Annelida - Hirudinea, incl. Acanthobdellea and Branchiobdellea. Biodiversity Data Journal 2: e4015. https://doi.org/10.3897/BDJ.2.e4015

Morton B, Velkovrh F, Sket B (1998) Biology and anatomy of the 'living fossil' *Congeria kusceri* (Bivalvia: Dreissenidae) from subterranean rivers and caves in the Dinaric karst of the former Yugoslavia. Journal of Zoology 245: 147–174. https://doi.org/10.1017/S0952836998006426

Pašić L, Kovče B, Sket B, Herzog-Velikonja B (2010) Diversity of microbial communities colonizing the walls of a Karstic cave in Slovenia. FEMS Microbiology Ecology 71: 50–60. https://doi.org/10.1111/j.1574-6941.2009.00789.x

Prevorčnik S, Blejec A, Sket B (2004) Racial differentiation in *Asellus aquaticus* (L.) (Crustacea: isopoda: Asellidae). Archiv fur Hydrobiologie 160: 193–214. https://doi.org/10.1127/0003-9136/2004/0160-0193

Prevorčnik S, Ferreira RL, Sket B (2012) Brasileirinidae, a new isopod family (Crustacea: Isopoda) from the cave in Bahia (Brazil) with a discussion on its taxonomic position. Zootaxa 3452: 47–65. https://doi.org/10.11646/zootaxa.3452.1.2

Prevorčnik S, Jugovic J, Sket B (2009) Geography of morphological differentiation in *Asellus aquaticus* (Crustacea: Isopoda: Asellidae). Journal of Zoological Systematics and Evolutionary Research 47: 124–131. https://doi.org/10.1111/j.1439-0469.2008.00493.x

Prevorčnik S, Konec M, Sket B (2016) The first *Turcolana* Argano & Pesce, 1980 (Isopoda: Cirolanidae) from the Greek mainland. Zootaxa 4170: 125–136. https://doi.org/10.11646/zootaxa.4170.1.6

Prevorčnik S, Sket B (2007) An ecologically peculiar new species of *Monolistra* (Crustacea: Isopoda: Sphaeromatidae) from the cave waters in the Dinaric karst of Croatia. Subterranean biology 5: 23–28.

Prevorčnik S, Verovnik R, Zagmajster M, Sket B (2010) Biogeography and phylogenetic relations within the Dinaric subgenus *Monolistra* (*Microlistra*) (Crustacea: Isopoda: Sphaeromatidae), with a description of two new species. Zoological Journal of the Linnean Society 159: 1–21. https://doi.org/10.1111/j.1096-3642.2009.00593.x

Sawicki TR, Holsinger JR, Sket B (2005) Redescription of the subterranean amphipod crustacean *Flagitopisa philippensis* (Hadzioidea: Melitidae), with notes on its unique morphology and clarification of the taxonomic status of *Psammogammarus fluviatilis*. The Raffles bulletin of zoology 53: 59–68.

Sidorov D, Zhonge H, Sket B (2018) Three new remarkable amphipod species (Crustacea: Gammaridae) from springs and subterranean waters of Central Asia. Zootaxa 4444: 437–461. https://doi.org/10.11646/zootaxa.4444.4.5

Simčič T, Sket B (2019) Comparison of some epigean and troglobiotic animals regarding their metabolism intensity. Examination of a classical assertion. International Journal of Speleology 48: 133–144. https://doi.org/10.5038/1827-806X.48.2.2251

Simčič T, Sket B (2021) Ecophysiological responses of two closely related epigean and hypogean *Niphargus* species to hypoxia and increased temperature: Do they differ? International Journal of Speleology 50: 111–120. https://doi.org/10.5038/1827-806X.50.2.2369

Sket B (1956) Einige Neue Formen der Malacostraca (Crust.) aus Jugoslawien. Bulletin scientifique. Section A, Sciences naturelles, techniques et medicales 3: 70–71.

Sket B (1958) Prispevek k poznavanju naših amfipodov. Biološki vestnik 6: 66–75.

Sket B (1960) Einige Neue Formen der Malacostraca aus Jugoslawien. III. Bulletin scientifique. Section A, Sciences naturelles, techniques et medicales 5: 73–75.

Sket B (1963) *Asellus slavus* Remy (Crust., Isopoda) v Jugoslaviji: (s 7 slikami v tekstu) = *Asellus slavus* Remy (Crust., Isopoda) in Jugoslawien: (mit 7 Abbildungen im Text). Razprave-Dissertationes, SAZU, Razred za prirodoslovne vede, cl. IV 7: 177–197.

Sket B (1964a) Genus *Sphaeromides* Dollfus 1897 (Crust., Isopoda, Cirolanidae) in Jugoslawien). Biološki vestnik 12: 153–168.

Sket B (1964b) Östliche gruppe der Monolistrini (Crust., Isopoda), I, Systematischer Teil. International Journal of Speleology 1: 163–189. https://doi.org/10.5038/1827-806X.1.1.14

Sket B (1965a) Östliche Gruppe der Monolistrini (Crust., Isopoda): II.Biologischer Teil. International Journal of Speleology 1: 249–267. https://doi.org/10.5038/1827-806X.1.3.1

Sket B (1965b) Taksonomska problematika vrste *Asellus aquaticus* (L.) Rac. (Crust., Isopoda) s posebnim ozirom na populacijo v Sloveniji. Slovenska akademija znanosti in umetnosti, razred za prirodoslovne in medicinske vede, Razprave-Dissertationes 8: 3–45.

Sket B (1968) K poznavanju favne pijavk (Hirudinea) v Jugoslaviji. Razprave-Dissertationes, SAZU, Razred za prirodoslovne vede, cl. IV 11: 129–197.

Sket B (1969) Eine Neue Art der Stenasellinae (Isopoda, Asselota) aus Senegal. Bulletin scientifique. Section A, Sciences naturelles, techniques et medicales 12: 386–387.

Sket B (1970) Predhodno poročilo o ekoloških raziskavah v sistemu kraške Ljubljanice. Biološki Vestnik 18: 79–87.

Sket B (1971) Vier Neue Aberrante *Niphargus*—Arten (Amphipoda, Gammaridae) und Einige Bemerkungen zur Taxonomie der *Niphargus*—ähnlichen Gruppen. Dissertationes Academia Scientiarum et Artium Slovenica - Classis IV: Historia Naturalis et Medicina 14: 1–25.

Sket B (1972) Die *Niphargus jovanovici*—Gruppe (Amphipoda, Gammaridae) in Jugoslawien und NO- Italien, Taxonomisch, Zoogeographisch und Phylogenetisch Betrachtet. Dissertationes Academia Scientiarum et Artium Slovenica - Classis IV: Historia Naturalis et Medicina 15: 99–140.

Sket B (1974) *Niphargus stygius* (Schiödte) (Amphipoda, Gammaridae)- die Neubeschreibung des Generotypus, Variabilität, Verbreitung und Biologie der Art, I. Biološki Vestnik 22: 91–103.

Sket B (1977) *Niphargus* im Brackwasser. Crustaceana. Supplement 4: 188–191.

Sket B (1979a) *Atlantasellus cavernicolus* n. gen., n. sp. (Isopoda Asellota, Atlantasellidae n. fam.) from Bermuda. Biološki vestnik 27: 175–183.

Sket B (1979b) Jamska favna Notranjskega trikotnika (Cerknica - Postojna - Planina), njena ogroženost in naravovarstveni pomen. Varstvo narave 13: 45–59.

Sket B (1981a) Distribution, ecological character and phylogenetic importance of *Niphargus valachicus* (Amphipoda, Gammaridae s. l.). Biološki vestnik 29: 87–103.

Sket B (1981b) *Niphargobates orophobata* n.g., n.sp. (Amphipoda, Gammaridae s.l.) from cave waters in Slovenia. Biološki vestnik 29: 105–118.

Sket B (1981c) Rhynchobdellid leeches (Hirudinea, Rhynchobdellae) in the relic Ohrid lake region. Biološki vestnik 29: 67–89.

Sket B (1982a) New Protojaniridae (Isopoda, Asellota) from Sri Lanka and some corrections of the taxonomy of the family. Biološki vestnik 30: 127–142.

Sket B (1982b) Some news about the subgenus *Microlistra* (Isopoda, Sphaeromatidae) in the subterranean waters of Yugoslavia. Biološki vestnik 30: 143–153.

Sket B (1985a) A contribution to the general morphology of Protojaniridae (Isopoda, Asellota) with some phylogenetic considerations concerning Asellota. Crustaceana 48: 200–208. https://doi.org/10.1163/156854085X00909

Sket B (1985b) *Piscicola hadzii* sp. n. (Piscicolidae, Hurudinea), a probably endemic species of leeches from Hercegovina, Yugoslavia. Biološki vestnik 33: 89–94.

Sket B (1985c) Why all cave animals do not look alike—a discussion on adaptive value of reduction processes. NSS Bulletin 47: 78–85.

Sket B (1986a) Ecology of the mixohaline hypogean fauna along Yugoslav coasts. Stygologia 2: 317–228.

Sket B (1986b) Evaluation of some taxonomically, zoogeographically, or ecologically interesting finds in the hypogean waters of Yugoslavia (in the last decades). Comunic., 9. Congr. Int. Espeleol 1: 126–128.

Sket B (1986c) Hirudinea. In: Botosaneanu L (Ed.) Stygofauna mundi: a faunistic, distributional and ecological synthesis of the world fauna inhabiting subterranean waters (including the Marine Insterstitial). Institute of Taxonomic Zoology, Amsterdam, 250–253. https://doi.org/10.1163/9789004631977_029

Sket B (1986d) Isopoda: Oniscidea. In: Botosaneanu L (Ed.) Stygofauna mundi: a faunistic, distributional and ecological synthesis of the world fauna inhabiting subterranean waters (including the Marine Insterstitial). Institute of Taxonomic Zoology, Amsterdam, 482–485. https://doi.org/10.1163/9789004631977_050

Sket B (1986e) Isopoda: Sphaeromatidae. In: Botosaneanu L (Ed.) Stygofauna mundi: a faunistic, distributional and ecological synthesis of the world fauna inhabiting subterranean

waters (including the Marine Insterstitial). Institute of Taxonomic Zoology, Amsterdam, 423–427. https://doi.org/10.1163/9789004631977_044

Sket B (1986f) O favni v Križni jami. Notranjski list 3: 25–27.

Sket B (1988) Zoogeografija sladkovodnih in somornih rakov (Crustacea) v kvarnersko-velebitskem območju. Biološki vestnik 36: 63–76.

Sket B (1989) Intralacustrine speciation in the genus *Dina* (Hirudinea, Erpobdellidae) in Lake Ohrid (Yugoslavia). Hydrobiologia 182: 49–59. https://doi.org/10.1007/BF00006367

Sket B (1990a) Is *Niphargobates lefkodemonaki* sp. n. (Crustacea: Amphipoda) from Kriti (Greece) a Zoogeographical Enigma? Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere 117: 1–10.

Sket B (1990b) Isopoda (Crustacea: Isopoda: *Microcharon*, *Jaera*, *Proasellus*) and other fauna in hypogean waters of southern Cyprus. International Journal of Speleology 19: 39–50. https://doi.org/10.5038/1827-806X.19.1.4

Sket B (1992a) Conservation of sites important their hypogean fauna - a proposal. Bulletin de liaison de la Société de biospéologie 19: 23–36.

Sket B (1992b) Distribution of Hirudunea (Annelida) in the ancient Ohrid Lake region. Archiv für Hydrobiologie 124: 225–237. https://doi.org/10.1127/archiv-hydrobiol/124/1992/225

Sket B (1992c) Rdeči seznam ogroženih pijavk (Hirudinea) v Sloveniji = The red list of endangered Hirudeinea in Slovenia. Varstvo narave : revija za teorijo in prakso varstva naravne dediščine 17.

Sket B (1992d) Rdeči seznam ogroženih sladkovodnih višjih rakov (Malacostraca aquatica) Isopoda, Amphipoda, Decapoda) v Sloveniji = The red data list endangered freshwater Malacostraca: (Isopoda aquatica, Amphipoda, Decapoda) in Slovenia. Varstvo narave: revija za teorijo in prakso varstva naravne dediščine 17: 147–155.

Sket B (1992e) Rdeči seznam ogroženih vrst dvoživk (Amphibia) v Sloveniji = The red list of endangered Amphibia in Slovenia. Varstvo narave : revija za teorijo in prakso varstva naravne dediščine 17.

Sket B (1992f) Rdeči seznam ogroženih živali podzemeljskih voda v Sloveniji = The red list of the inhabitants of hypogean waters in Slovenia. Varstvo narave : revija za teorijo in prakso varstva naravne dediščine 17: 193–204.

Sket B (1994a) Distribution of *Asellus aquaticus* (Crustacea: Isopoda: Asellidae) and its hypogean populations at different geographic scales , with a note on Proasellus istrianus. Hydrobiologia 287: 39–47. https://doi.org/10.1007/BF00006895

Sket B (1994b) Distribution patterns of some subterranean Crustacea in the territory of the former Yugoslavia. Hydrobiologia 287: 65–75. https://doi.org/10.1007/BF00006897

Sket B (1996a) Pijavke (Hirudinea) - stanje in ogroženost favne = Leeches (Hirudinea) in Slovenia - present condition of the fauna and threats. In: Gregori J (Ed.) Narava Slovenije, stanje in perspektive : zbornik prispevkov o naravni dediščini Slovenije. Ljubljana, 219–221.

Sket B (1996b) The ecology of anchihaline caves. Trends in Ecology and Evolution 11: 221–225. https://doi.org/10.1016/0169-5347(96)20031-X

Sket B (1997) Distribution of *Proteus* (Amphibia: Urodela: Proteidae) and its possible explanation. Journal of Biogeography 24: 263–280. https://doi.org/10.1046/j.1365-2699.1997.00103.x

Sket B (1999a) High biodiversity in hypogean waters and its endangerment - the situation in Slovenia, the Dinaric Karst, and Europe. Crustaceana 72: 767–779. https://doi.org/10.1163/156854099503951

Sket B (1999b) *Niphargus aquilex dobati* ssp. n. (Crustacea) from the karst of Slovenia. Mitt. Verb. dt. Hoehlen- u. Karstforsch 45: 54–56.

Sket B (1999c) The nature of biodiversity in hypogean waters and how it is endangered. Biodiversity and Conservation 8: 1319–1338. https://doi.org/10.1023/A:1008916601121

Sket B (2000) *Fuxiana yangi* g.n., sp.n. (Crustacea: Amphipoda), a "baikaloid" amphipod from the depths of Fuxian Hu, an ancient lake in the karst of Yunnan, China. Archiv fur Hydrobiologie 147: 241–255. https://doi.org/10.1127/archiv-hydrobiol/147/1999/241

Sket B (2002) The evolution of the karst versus the distribution and diversity of the hypogean fauna. In: Gabrovšek F (Ed.) Evolution of Karst: From Prekarst to Cessation. Karst Research Institute ZRC SAZU, Postojna, 225–232.

Sket B (2004) The cave hygropetric – a little known habitat and its inhabitants. Archiv fur Hydrobiologie 160: 413–425. https://doi.org/10.1127/0003-9136/2004/0160-0413

Sket B (2008a) A contribution to the history of biodiversity research in Slovenia – lower invertebrates mainly. Acta Biologica Slovenica 51: 5–19. https://doi.org/10.14720/abs.51.2.15244

Sket B (2008b) Can we agree on an ecological classification of subterranean animals? Journal of Natural History 42: 1549–1563. https://doi.org/10.1080/00222930801995762

Sket B (2011) Izvor dinarske troglobiotske školjke in njena pravilna taksonomska uvrstitev. *Congeria* ali *Mytilopsis* (Bivalvia: Dreissenidae)? Acta Biologica Slovenica 54: 67–76. https://doi.org/10.14720/abs.54.1.15473

Sket B (2012) *Merozoon vestigatum* g. n., sp. n., a new freshwater subterranean isopod (Isopoda: Sphaeromatidae) from a cave in Croatia. Acta Biologica Slovenica 55: 71–76. https://doi.org/10.14720/abs.55.2.15538

Sket B (2018) Collecting and processing crustaceans of subterranean habitats. Journal of Crustacean Biology 38: 380–384. https://doi.org/10.1093/jcbiol/rux125

Sket B, Velikonja M (1986) Troglobitic freshwater sponges (Porifera, Spongillidae) found in Yugoslavia. Stygologia 2: 254–266.

Sket B, Arntzen JW (1994) A black, non-troglomorphic amphibian from the karst of Slovenia: *Proteus anguinus parkelj* (Urodela: Proteidae). Bijdragen tot de Dierkunde 64: 33–53. https://doi.org/10.1163/26660644-06401002

Sket B, Baratti M (2021) Phylogenetic relationships of *Sphaeromides* Dollfus, 1897 (Crustacea: Isopoda: Cirolanidae) and some related taxa, with new considerations about *Trogloaega* Brian, 1923. Journal of Natural History 55: 1663–1679. https://doi.org/10.1080/00222933.2021.1952328

Sket B, Bole J, Benović A, Brancelj A, Brglez J, Čuček M, Čurčić B, Jaklin A, Karaman GS, Katavić I, Kerovac M, Kos I, Legac M, Mršić N, Malej A, Novak T, Petkovski S, Petkovski T, Polenec A, Potočnik F, Pujin V, Radujkovič B, Ševčić Z, Tarman K, Travizi A, Velikonja M, Velkovrh F, Vidaković J, Zavodnik D (1991) Richness and state of knowledge of the fauna of Yugoslavia: lower invertebrates (Metazoa: Invertebrata, ex. Insecta. Biološki vestnik 31: 37–52.

Sket B, Brancelj A (1992) Rdeči seznam ogroženih sladkovodnih nižjih rakov (Entomostraca: Anostraca, Cladocera, Copepoda, Ostracoda) v Sloveniji = The red list of freshwater

Entomostraca (Anostraca, Cladocera, Copepoda, Ostracoda) in Slovenia. Varstvo narave: revija za teorijo in prakso varstva naravne dediščine 17: 165–172.

Sket B, Bruce NL (2004) Sphaeromatids (Isopoda, Sphaeromatidae) from New Zealand fresh and hypogean waters, with description of *Bilistra* n. gen. and three new species. Crustaceana 76: 1347–1370. https://doi.org/10.1163/156854003323009858

Sket B, Dovč P, Jalžić B, Kerovec M, Kučinić M, Trontelj P (2001) A cave leech (Hirudinea, Erpobdellidae) from Croatia with unique morphological features. Zoologica Scripta 30: 223–229. https://doi.org/10.1046/j.1463-6409.2001.00065.x

Sket B, Fišer C (2009) A new case of intralacustrine radiation in amphipoda. A new genus and three new species of anisogammaridae (crustacea, amphipoda) from the ancient lake Fuxian Hu in Yunnan, China. Journal of Zoological Systematics and Evolutionary Research 47(2): 115–123. https://doi.org/10.1111/j.1439-0469.2008.00477.x

Sket B, Hou Z (2018a) Family Gammaridae (Crustacea: Amphipoda), mainly its *Echinogammarus* clade in SW Europe. Further elucidation of its phylogeny and taxonomy. Acta Biologica Slovenica 61: 93–102. https://doi.org/10.14720/abs.61.2.15898

Sket B, Hou (2018b) Family Gammaridae (Crustacea: Amphipoda), mainly its Echinogammarus clade in SW Europe. Further elucidation of its phylogeny and taxonomy Družina Gammaridae (Crustacea: Amphipoda), posebej njena veja Echinogammarus v JZ Evropi. Nadaljnja razjasnitev filog. Acta Biologica Slovenica 61: 93–102. https://doi.org/10.14720/abs.61.2.15898

Sket B, Karaman GS (1990) *Niphargus rejici* (Amphipoda), its relatives in the Adriatic islands, and its possible relations to S.W. Asian taxa. Stygologia 5.

Sket B, Karaman GS (2018) Phylogenetic position of the genus *Chaetoniphargus* Karaman et Sket (Crustacea: Amphipoda: Niphargidae) from Dinaric Karst. An extreme case of homoplasy. Folia Biologica et Geologica 59: 93–99. https://doi.org/10.3986/fbg0046

Sket B, Notenboom J (1993) Phylogeny and biogeography of the *Niphargus transitivus* group of species (Crustacea, Amphipoda). Bijdragen tot de Dierkunde 63: 149–161. https://doi.org/10.1163/26660644-06303002

Sket B, Paragamian K, Trontelj P (2004a) A census of the obligate subterranean fauna of the Balkan Peninsula. In: Krystufek B, Reed JM (Eds) Balkan biodiversity: Pattern and process in the European hotspot. Kluwer Academic Press, 309–322. https://doi.org/10.1007/978-1-4020-2854-0_18

Sket B, Sidorov D, Hou Z (2019) What happened to the genus *Gammarus* (Crustacea: Amphipoda) in Central Asia. Acta Biologica Slovenica 62: 45–66. https://doi.org/10.14720/abs.62.2.15754

Sket B, Šapkarev J (1986) *Dina lepinja* sp. n. (Hirudinea, Erpobdellidae), a new endemic leech from the ancient lake Ohridsko jezero. Biološki vestnik 34: 89–92.

Sket B, Trontelj P (2008) Global diversity of leeches (Hirudinea) in freshwater. Hydrobiologia 595: 129–137. https://doi.org/10.1007/s10750-007-9010-8

Sket B, Trontelj P, Žagar C (2004b) Speleobiological characterization of the epikarst and its hydrological neighborhood: its role in dispersion of biota, its ecology and vulnerability. In: Jones K, Culver DC, Herman JS (Eds) Epikarst. Proceedings of the symposium October 1-4, 2003, Shepherdstown, West Virginia, USA. Karst Waters Institute, Charles Town, 104–113.

Sket B, Velkovrh F (1981a) Phreatische Fauna in Ljubljansko polje (Ljubljana-Ebene, Jugoslawien) – ihre ökologische Verteilung und zoogeographische Beziehungen. International journal of Speleology 11: 105–121. https://doi.org/10.5038/1827-806X.11.1.11

Sket B, Velkovrh F (1981b) Postojnsko-Planinski jamski sistem kot model za preučevanje onesnaženja podzemeljskih voda. Naše jame 22: 27–44.

Sket B, Zakšek V (2009) European cave shrimp species (Decapoda: Caridea: Atyidae), redefined after a phylogenetic study; redefinition of some taxa, a new genus and four new *Troglocaris* species. Zoological Journal of the Linnean Society 155(4): 786–818. https://doi.org/10.1111/j.1096-3642.2008.00473.x

Stock JH, Sket B, Iliffe TM (1987) Two new amphipod crustaceans from anchihaline caves in Bermuda. Crustaceana 53: 54–66. https://doi.org/10.1163/156854087X00628

Trontelj P, Douady CJ, Fišer C, Gibert J, Gorički Š, Lefébure T, Sket B, Zakšek V (2009) A molecular test for cryptic diversity in ground water: How large are the ranges of macro-stygobionts? Freshwater Biology 54: 727–744. https://doi.org/10.1111/j.1365-2427.2007.01877.x

Trontelj P, Gorički Š, Polak S, Verovnik R, Zakšek V, Sket B (2007) Age estimates for some subterranean taxa and lineages in the Dinaric Karst. Acta Carsologica 36: 183–189. https://doi.org/10.3986/ac.v36i1.220

Trontelj P, Sket B (2000) Molecular re-assessment of some phylogenetic, taxonomic and biogeographic relationships between the leech genera *Dina* and *Trocheta* (Hirudinea: Erpobdellidae). Hydrobiologia 438: 227–235. https://doi.org/10.1023/A:1004137300113

Trontelj P, Sket B, Dovc P, Steinbrück G (1996) Phylogenetic relationships in European erpobdellid leeches (Hirudinea: Erpobdellidae) inferred from restriction-site data of the 18S ribosomal gene and ITS2 region. Journal of Zoological Systematics and Evolutionary Research 34: 85–93. https://doi.org/10.1111/j.1439-0469.1996.tb00813.x

Trontelj P, Sket B, Steinbrück G (1999) Molecular phylogeny of leeches: Congruence of nuclear and mitochondrial rDNA data sets and the origin of bloodsucking. Journal of Zoological Systematics and Evolutionary Research 37: 141–147. https://doi.org/10.1111/j.1439-0469.1999.tb00976.x

Turk S, Sket B, Sarbu SM (1996) Comparison between some epigean and hypogean populations of *Asellus aquaticus* (Crustacea: Isopoda: Asellidae). Hydrobiologia 337: 161–170. https://doi.org/10.1007/BF00028517

Väinölä R, Witt JDS, Grabowski M, Bradbury JH, Jazdzewski K, Sket B (2008) Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. Hydrobiologia 595: 241–255. https://doi.org/10.1007/s10750-007-9020-6

Verovnik R, Sket B, Prevorčnik S, Trontelj P (2003) Random amplified polymorphic DNA diversity among surface and subterranean populations of *Asellus aquaticus* (Crustacea: Isopoda). Genetica 119: 155–165. https://doi.org/10.1023/A:1026085716777

Verovnik R, Sket B, Trontelj P (2004) Phylogeography of subterranean and surface populations of water lice *Asellus aquaticus* (Crustacea: Isopoda). Molecular Ecology 13: 1519–1532. https://doi.org/10.1111/j.1365-294X.2004.02171.x

Verovnik R, Sket B, Trontelj P (2005) The colonization of Europe by the freshwater crustacean *Asellus aquaticus* (Crustacea: Isopoda) proceeded from ancient refugia and was directed by

habitat connectivity. Molecular Ecology 14: 4355–4369. https://doi.org/10.1111/j.1365-294X.2005.02745.x

Verovnik R, Trontelj P, Sket B (1999) Genetic differentiation and species status within the snail leech *Glossiphonia complanata* aggregate (Hirudinea: Glossiphoniidae) revealed by RAPD analysis. Archiv für Hydrobiologie 144: 327–338. https://doi.org/10.1127/archiv-hydrobiol/144/1999/327

Zagmajster M, Culver DC, Christman MC, Sket B (2010) Evaluating the sampling bias in pattern of subterranean species richness: Combining approaches. Biodiversity and Conservation 19: 3035–3048. https://doi.org/10.1007/s10531-010-9873-2

Zagmajster M, Culver DC, Sket B (2008) Species richness patterns of obligate subterranean beetles (Insecta: Coleoptera) in a global biodiversity hotspot - Effect of scale and sampling intensity. Diversity and Distributions 14: 95–105. https://doi.org/10.1111/j.1472-4642.2007.00423.x

Zagmajster M, Turjak M, Sket B (2012) Database on subterranean biodiversity of the Dinarides and neighboring regions- SubBioDatabase. In: Kováč L (Ed.) 21st International Conference on Subterranean Biology, 2–7 September, 2012, Košice, Slovakia. Pavol Jozef Šafárik University, Košice, Slovakia, 114–115.

Zakšek V, Sket B, Gottstein S, FranjeviĆ D, Trontelj P (2009) The limits of cryptic diversity in groundwater: Phylogeography of the cave shrimp *Troglocaris anophthalmus* (Crustacea: Decapoda: Atyidae). Molecular Ecology 18: 931–946. https://doi.org/10.1111/j.1365-294X.2008.04061.x

Zakšek V, Sket B, Trontelj P (2007) Phylogeny of the cave shrimp *Troglocaris*: Evidence of a young connection between Balkans and Caucasus. Molecular Phylogenetics and Evolution 42: 223–235. https://doi.org/10.1016/j.ympev.2006.07.009

Supplementary material 1

Bibliography of Boris Sket

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